SIZE, GROWTH, DEVELOPMENT, AND SURVIVAL OF THE PLANKTONIC LARVAE OF *POMATOMUS SALTATRIX* (PISCES: POMATOMIDAE)

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Abstract. A variety of hypotheses have been proposed regarding the processes that regulate survival of the planktonic life history stages of marine organisms. Several of these hypotheses have been grouped under a general, "growth–mortality" hypothesis, which postulates that larger (a "bigger-is-better" mechanism), faster growing (a "growth-rate" mechanism), and faster developing (a "stage-duration" mechanism) individuals have a higher probability of survival. Using the otolith record of age, size, and ontogeny, these three mechanisms of the "growth–mortality" hypothesis were tested for the larval and pelagic juvenile stages of bluefish, *Pomatomus saltatrix* (Pisces: Pomatomidae), a moderate-sized, coastal, pelagic, marine fish. Individuals that were larger-at-age were found to have a higher probability of survival, supporting the "bigger-is-better" mechanism. Faster growing individuals were also found to have a higher probability of survival, agreeing with the prediction of the "growth-rate" mechanism. Equivocal evidence was found with regard to the "stage-duration" mechanism. These results suggest that in pelagic ecosystems, larger and faster growing larvae have a higher probability of survival. Given the observed directional selection acting on larval size and growth, several potential mechanisms that maintain variable larval size and growth are addressed. Finally, the growth-related processes examined in this study are discussed in the context of the physical aspects of pelagic ecosystems that may also affect larval survival.

Key words: bluefish; body size; development rate; growth rate; larval ecology; marine ecosystems; phenotypic selection; planktonic survival; Pomatomus saltatrix; *population biology; recruitment; selective mortality.*

INTRODUCTION

Size-spectrum theory proposes that the concentration of organisms in pelagic ecosystems decreases as size increases (Sheldon et al. 1972, 1973, Conover 1978, Platt and Denman 1978). Coinciding with this decrease in concentration, mortality rate decreases as organism size increases, presumably since there are fewer predators at larger sizes (Peterson and Wroblewski 1984, McGurk 1986, 1993). An implication of this size structure is that the probability of mortality will be relatively constant through time for species that grow little during their life cycle. On the other hand, for species that undergo substantial growth relative to the pelagic size spectrum, the probability of mortality will decrease as size increases. This latter group includes the larvae of many marine fishes and benthic marine invertebrates whose life histories are characterized by small, planktonic eggs and larvae, which after a period of growth and development, "metamorphose" to juvenile forms and enter juvenile habitats (Thorson 1950, Leis 1991).

A widely held view of the population dynamics of marine fishes and marine benthic invertebrates is that

the number of offspring surviving to the larval–juvenile transition greatly influences future patterns in adult abundance (Underwood and Denley 1984, Gaines and Roughgarden 1985, Rothschild 1986, Jones 1991, Leggett and DeBlois 1994). Early this century, Hjort (1914) proposed that the number of fish larvae surviving to the end of the planktonic stage was determined by feeding success immediately following the depletion of maternally provided nutrition (i.e., the transition between yolk sac and feeding larvae). A variety of related starvation, food abundance, and feeding success hypotheses have since been proposed (e.g., Lasker 1978, Paulay et al. 1985). Alternatively, many studies have documented the importance of predation as a source of larval mortality (e.g., Gaines and Roughgarden 1987, Arai 1988, Purcell 1989), but the relative role of predation, starvation, and feeding success in determining larval survival remains unresolved (see May 1974, Anderson 1988, Bailey and Houde 1989, Leggett and DeBlois 1994).

The "growth–mortality" hypothesis combines feeding success and predation into one integrated framework: as feeding success increases, growth increases and the probability of mortality due to starvation and predation decreases (see Anderson 1988). Three, nonexclusive mechanisms have been proposed for the functional basis of the "growth–mortality" hypothesis. First, if mortality is size dependent, then the larger

individuals of a given age will have a lower probability of mortality compared to smaller individuals of the same age (i.e., a "bigger-is-better" mechanism, see Leggett and DeBlois 1994). Second, if the probability of mortality is a decreasing function of size, then higher growth rates will minimize the time over which individuals experience higher mortality rates and thus, faster growing larvae will have a lower probability of mortality compared to slower growing larvae (i.e., a "growth-rate" mechanism; see Ware 1975, Shepherd and Cushing 1980). Third, if juveniles have a lower mortality rate compared to larvae, then individuals that develop faster and make the larval-to-juvenile transition at younger ages would have a lower probability of mortality compared to individuals that make the larval–juvenile transition at older ages (a "stage-duration" mechanism; Chambers and Leggett 1987, Houde 1987). These mechanisms are distinct in terms of the basis of selective mortality, but are potentially related by the extent to which larval size, growth rate, and development rate are correlated on an individual basis.

The "growth–mortality" hypothesis is supported by a variety of studies. Laboratory research has found that larger larvae are better able to avoid predation, obtain food, and resist starvation (see Hunter 1981, Miller et al. 1988, Bailey and Houde 1989). Field studies have shown that surviving individuals were larger at younger ages compared to the population as a whole (e.g., freshwater: Post and Prankevicius 1987, West and Larkin 1987; marine: Tsukamoto et al. 1989, DeVries et al. 1990, Meekan and Fortier 1996). Field studies have also shown that faster growing cohorts of larvae exhibit higher rates of survival (e.g., Graham and Townsend 1985, Castro and Cowen 1991).

Recently, however, a growing body of work has refuted certain aspects of the "growth–mortality" hypothesis. In the laboratory, individual predators often select larger prey items, indicating size-selective predation opposite to that expected under the "bigger-is-better" mechanism (Litvak and Leggett 1992, Pepin et al. 1992). From field data, Hoenig et al. (1990) concluded that late hatching, smaller larvae survived a given calendar period better than early hatching, larger larvae, again data contrary to the "bigger-is-better" mechanism. In addition, several field studies have found no evidence for size-selective larval mortality (e.g., freshwater, Post and Prankevicius 1987; marine, Laidig et al. 1991, Brown and Bailey 1992). Finally, opposite to expectations based on the "growth-rate" mechanism, interspecific correlations show that faster growing larvae have higher mortality rates (e.g., Houde 1989, Morse 1989, Pepin 1991).

Part of the uncertainty arises because few field studies have directly evaluated the "growth–mortality" hypothesis for a cohort of larvae. A "cohort of larvae" is broadly defined as a group of larvae hatched at similar times, which experience a similar pelagic environment. The temporal scale of a cohort is the period from

spawning to the larval–juvenile transition and the spatial scale is the area occupied over this time. It is at these scales, within pelagic ecosystems, that the interaction between growth and mortality must be examined.

The purpose of this study was to evaluate the three mechanisms of the "growth-mortality" hypothesis for a cohort of bluefish, *Pomatomus saltatrix* (Pisces: Pomatomidae), larvae spawned on the Middle Atlantic Bight continental shelf (Cape Hatteras, North Carolina to Cape Cod, Massachusetts). *P. saltatrix* is a moderate-sized (<10 kg) coastal pelagic marine fish that makes annual north–south migrations along the eastern seaboard of the United States (Juanes et al. 1996). Our specific objectives were fourfold: (1) to determine whether larger individuals at a given age (i.e., individuals larger-at-age) had a higher probability of survival (i.e., the "bigger-is-better" mechanism), (2) to determine whether faster growing individuals had a higher probability of survival (i.e., the "growth-rate" mechanism), (3) to determine whether individuals that had a shorter larval stage had a higher probability of survival (i.e., the "stage-duration" hypothesis), and (4) to calculate the correlations among larval size, growth rate, and development rate in order to assess the ability of the above three mechanisms to act independently.

A cross-sectional analysis (sensu Cock 1966), also termed a comparison among age classes (sensu Endler 1986), was used to examine phenotypic selection acting on larval size, growth rate, and development rate. Cross-sectional data consist of a set of measurements made from individuals of different ages. If the traits measured are unmodified with age or growth (e.g., vertebrae number; Swain 1992*a*, *b*), then phenotypic selection acting on a given trait can be examined by comparing the frequency distribution of the trait among age classes. The null hypothesis is that age classes differ only by chance in their trait frequency distribution. The alternative hypothesis is that trait distributions differ significantly among age classes, indicating phenotypic selection. The "type" of selection (i.e., directional, stabilizing, disruptive) can then be inferred from the specific changes in the trait distributions with age (see Endler 1986).

Fish larvae are well suited for cross-sectional analyses (see Methot 1983, Crecco and Savoy 1987, Rice et al. 1987) since detailed age, size, and developmental histories are permanently recorded in their otoliths (Fig. 1), which are proteinaceous, carbonate structures analogous to mammalian earbones (see Campana and Nielsen 1985, Stevenson and Campana 1992 for general reviews). Otolith growth is concentric around a center of accretion and occurs through differential deposition of calcium carbonate and protein over a 24-h period, resulting in a daily, bipartite structure termed an otolith increment. Once deposited, material in an otolith remains unmodified and thus, certain traits measured from an otolith satisfy the requirement of cross-
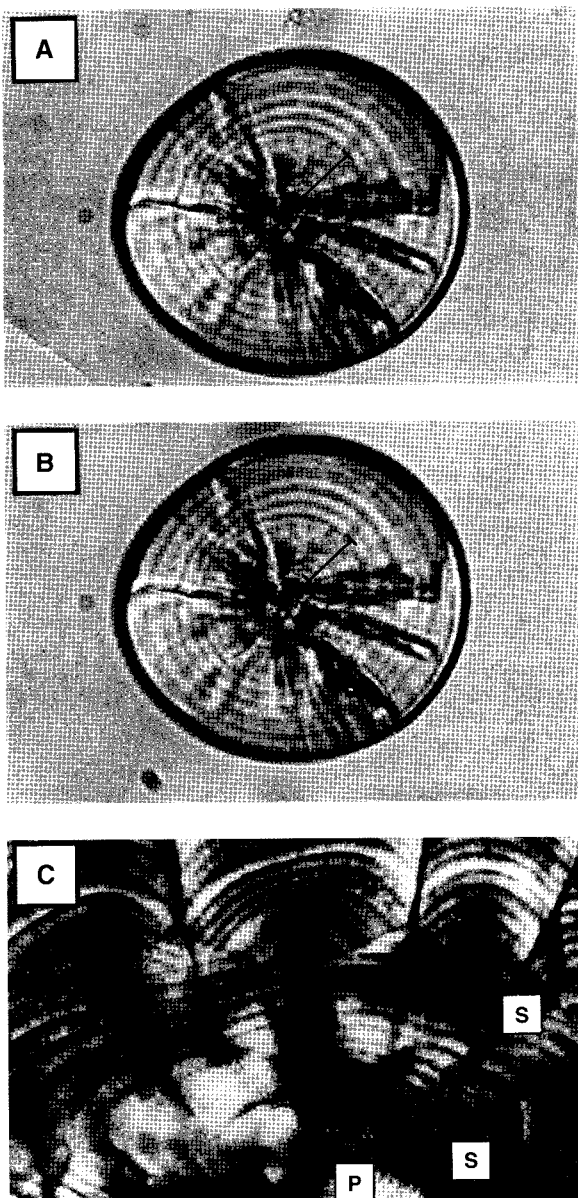
FIG. 1.　(A) The radius to a given otolith increment is a measure of the relative size of the larva on the day the increment was deposited (i.e., a larva with a larger otolith radius to increment 7 was larger in size on day 7 compared with a larva with a smaller otolith radius to increment 7). A radius is drawn from the center of primary otolith growth to increment 7. (B) The distance between otolith increments is a relative measure of the growth of the larva between the two days on which the increments were deposited (i.e., a larva with a larger otolith width between increments 2 and 7 grew faster from day 2 to day 7 than a larva with a smaller otolith width between increments 2 and 7). The edge of the primary primordia is the first mark from the center, then the second and seventh increments are marked. (C) Initially, otolith growth occurs around one primary center of growth (P). In *P. saltatrix*, secondary centers of otolith growth (S) begin to form at the edge of the otolith at the time when the larva undergoes the transition to juvenile (Hare and Cowen 1994). By enumerating the number of increments from the primary growth center to the first secondary growth center, the age at the larval–juvenile transition can be estimated. Photograph in panel C used with permission from Nyman (1987).

sectional analyses, namely that a trait remains unmodified with age. Since otolith increment formation is daily in most species (Campana and Nielson 1985, for a general review; Nyman and Conover 1988, Hare and Cowen 1994 for *Pomatomus saltatrix*), enumeration of the number of increments provides an estimate of the age of a larva. The radius of the otolith from the center to a given otolith increment (i.e., otolith radii-at-increment) yields an estimate of the relative size of a larva on the day the increment was deposited (Fig. 1A) and the distance between two increments provides a relative measure of somatic growth between the two days on which the two otolith increments were deposited (Fig. 1B; Campana 1990, Hare and Cowen 1995). In addition, different types of marks are deposited on the otolith at life history stage transitions: first-increment deposition occurs at hatching in some species, including *P. saltatrix,* and secondary centers of otolith growth form at the transition from larva to juvenile in a variety of species, again including *P. saltatrix* (Fig. 1C; Hare and Cowen 1994). Thus, the microstructure of the otolith (otolith radius to a specific increment, otolith radii between specific increments, and the increment at which secondary growth centers begin to form) provides a history of an individual's age, size, growth, and development that can be used in cross-sectional analyses.

The "bigger-is-better" and "growth-rate" mechanisms were evaluated using the otolith radius to specific increments (as a measure of fish size on the day the increment was deposited) and otolith growth between specific increments (as a measure of fish growth between specific days) respectively. If mortality results in directional phenotypic selection for larger individuals, otolith radii-at-increment should increase with increasing larval age (Fig. 2). Likewise, if mortality results in directional phenotypic selection for faster growing larvae, otolith growth over a certain period should increase with increasing larval age (Fig. 2). Endler (1986) indicated that under directional selection, the variance of a trait should decrease, but changes in variance are dependent on the specific form of selection (Fig. 2) and thus, predictions were not made with regard to variance.

The "stage-duration" mechanism was evaluated by comparing the results of a phenotypic selection model with the observed age at the larval–juvenile transition derived from the ontogenetic record contained within the otoliths of *Pomatomus saltatrix.* If there is a substantial decrease in mortality rate associated with the transition from larva to juvenile, then individuals that make the transition earlier will have a higher probability of survival compared to individuals that make the transition later (Fig. 3) (see also Houde 1987). This prediction was evaluated using a cross-sectional analysis of the age-at-transition; the "after-selection" distribution was based on the number of otolith increments prior to the formation of secondary growth centers and

**Otolith Radius to a Specific Increment (μm) or
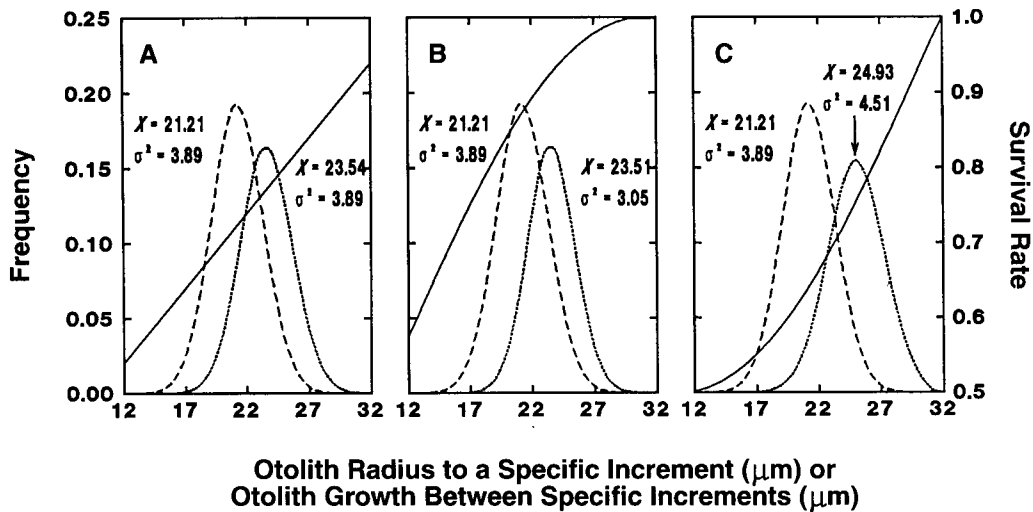Otolith Growth Between Specific Increments (μm)**

FIG. 2. A graphical representation of the predictions based on the "bigger-is-better" and "growth-rate" mechanisms of the growth–mortality hypothesis. In terms of the "bigger-is-better" mechanism, a distribution of otolith radii at increment A at time t (– – –, "before-selection" distribution) is subjected to three size-dependent survival functions (———, panels A, B, and C), which simulate the predicted directional selection favoring individuals that are larger at age A. The resulting "after-selection" distributions of otolith radius at increment A at a later time, $t + 1$, (········) are shown. As indicated by Endler (1986), the mean of a quantitative trait (e.g., otolith radius at increment A) increases under directional selection (the "before-selection" mean and variance are given to the left in each panel, the "after-selection" mean and variance are given to the right in each panel). Thus, under the "bigger-is-better" mechanism, it was predicted that mean otolith radius-at-increment will increase as the age of a larval cohort increases. Using the same arguments, it was predicted that under the "growth-rate" mechanism, otolith growth between specific increments will increase as the age of the larval cohort increases. Predictions were not made regarding variance since changes in variance depend on the specific form of directional selection. For example, the survival function used in panel A did not result in a change in variance, while the survival function in panel C resulted in an increase in variance. For this graphical representation, the "before-selection" distribution was assumed to be normal and the "after-selection" distributions were calculated using an negative exponential model $N_a = N_b e^{-Zt}$, where N_a is the "after selection" distribution (········), N_b is the "before-selection" distribution (– – –), t is time between samples (taken to be 30 d), and Z is the mortality rate (1 − survival rate), which is determined from the survival function (———).

the "before-selection" distribution was derived from a model based on age-at-transition data of laboratory-reared *Pseudopleuronectes americanus* (Chambers and Leggett 1987).

The correlation among larval size, growth rate, and development rate determines the degree to which the "bigger-is-better," "growth-rate" and "stage-duration" mechanisms can operate independently (see Lande and Arnold 1983). If larvae that are relatively small at a given age grow faster than larvae that are relatively large at a given age, then selection on size and growth rate can operate separately. Likewise, if fast-growing larvae make the larval–juvenile transition at later ages compared to slow-growing larvae, then the "growth-rate" and "stage-duration" mechanisms can act independently. To examine the potential independence of the three mechanisms of the "growth–mortality" hypothesis, Pearson correlation coefficients were calculated between otolith radii, otolith growth, and age at the larval–juvenile transition.

MATERIALS AND METHODS

Collection of larvae and otolith procedures

During the summer, *Pomatomus saltatrix* spawn on the continental shelf from Cape Hatteras, North Car-

olina to Cape Cod, Massachusetts (Smith et al. 1994), an area of ≈110 000 km². The scale of sampling for this work was limited by practical considerations to ≈40 000 km², covering the shelf from Montauk Point, New York to Cape May, New Jersey. Four cruises were conducted during the summer of 1988, each consisting of 49 sampling stations. Owing to weather and time constraints, not all stations were sampled during each cruise; a total of 175 stations were occupied. Larval and pelagic juvenile *P. saltatrix* were collected using two gears: a 1-m² Tucker Trawl with 505-μm mesh and a 5-m² modified-Methot Frame Trawl with 2-mm mesh (see Hare and Cowen 1991, Cowen et al. 1993 for more detail).

Otolith extraction and processing procedures are also described in detail elsewhere (Hare and Cowen 1994, 1995). Individuals ($n = 194$) were chosen from ichthyoplankton samples to represent the larval and pelagic juvenile size range collected, from 2-mm post yolk-sac larvae to 25-mm pelagic juveniles. Sagittal otoliths (Fig. 1) were extracted and examined three times in random order at 400×. Each examination included enumeration of the number of otolith increments (an estimate of the age of an individual), measurement of the otolith radius to each increment (a relative estimate of
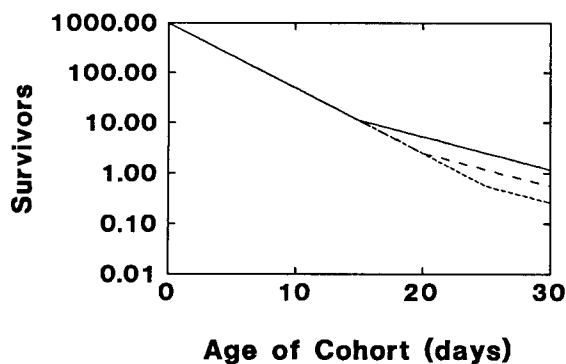
FIG. 3. A graphical representation of the "stage duration" mechanism of the growth–mortality hypothesis. Three cohorts of larvae are illustrated. Each cohort starts with the same number of individuals and is subjeced to negative exponential mortality, as is typically observed in pelagic systems (Peterson and Wroblewski 1984, McGurk 1986, 1993). In all cases, larval mortality rate $(Z_L = 0.3)$ is greater than the juvenile mortality rate $(Z_J = 0.15)$, but the age at the larval–juvenile transition (T_M) varies from 15 to 25 d. For the cohort that makes the transition at 15 d (———), about 1 in 1000 indivdiuals survive to day 30. For the cohort that makes the transition at 20 d (– – –), about 0.75 in 1000 individuals survive to day 30. For the cohort that makes the transition at 25 d (·······), about 0.5 in 1000 individuals survive to day 30. Thus, if the larval mortality rate is higher than the juvenile mortality rate, one would predict that individuals making the larval–juvenile transition earlier will have a higher probability of survival (e.g., the "stage-duration" mechanism). For this graphical representation, a negative exponential model was used to estimate the number of survivors over time: $N_t = N_0 e^{-Z_L t}$ for $t < T_M$ and $N_t = N_0 e^{-Z_L T_M} e^{-Z_J (t - T_M)}$ for $t > T_M$, where N_t is the number of individuals surviving to time t, N_0 is the initial number of individuals at time 0, taken as 1000, Z_L is larval mortality rate (0.3 d^{-1}), Z_J is juvenile mortality rate (0.15 d^{-1}), and T_M is the age-at-transition (15, 20, or 25 d).

the size of an individual on each day), and enumeration of the increment of origin of secondary growth centers, if present (an estimate of the age of an individual at the larval–juvenile transition). Precision in otolith increment counts was examined to identify potential aging errors (Campana and Mokness 1991). If the standard deviation of increment counts for an individual was >1 and the coefficient of variation was >10%, the otolith was reexamined twice more (this was the case for 25 individuals). The resulting five otolith increment counts were compared, and the data associated with the two outlying counts were discarded. Age was then estimated for all individuals from the mean of three increment counts. Mean and standard deviation of the radius to each increment were also calculated. Additionally, the mean and standard deviation were calculated for the distance between specific otolith increments: 1–5, 5–10, 10–15, and 15–20. Finally, the mean number of otolith increments prior to secondary growth center formation was enumerated. Otolith radius measurements were made along the maximum otolith radius with the aid of image analysis software (Optical

Pattern Recognition System, Biosonics, Seattle, Washington). The maximum otolith radius was aligned to the horizontal on the video system to prevent bias owing to measurement orientation.

Tests of the "bigger-is-better" and "growth-rate" mechanisms

The prediction based on the "bigger-is-better" mechanism (i.e., larger larvae at a given age have a higher probability of survival) was tested by determining whether the distribution of otolith radii-at-increment, as a measure of larval size, changed with increasing age. Fish were assigned to six age classes: 0–5 d $(n = 16)$, 5–10 d $(n = 73)$, 10–15 d $(n = 41)$, 15–20 d $(n = 30)$, 20–25 d $(n = 19)$, and >25 d $(n = 15)$ and a repeated-measures analysis of variance (ANOVA) was calculated to test for age class differences in the radius to particular otolith increments (1, 5, 10, 15, and 20). The three measures of otolith radii were treated as repeated measures. All pairwise comparison of means among age classes were made using a Bonferroni correction (significance value [$\alpha = 0.05$]/number of comparisons made; Sokal and Rohlf 1981, Wilkinson 1990). Preliminary examination of otolith radius data indicated that variance increased with age; a log-transformation successfully homogenized variances.

The "growth-rate" mechanism (i.e., faster growing larvae have a lower probability of mortality compared to slower growing larvae) was evaluated by determining whether the distribution of otolith growth between specific increments, as a measure of larval growth, increased with increasing age. Again, a repeated-measures ANOVA was used with the same age groups as above. Otolith growth between increments 1–5, 5–10, 10–15, 15–20, and 20–25 was analyzed for differences between age classes. The 0–5 d age class was not used because the width of the otolith between increment 1 and 5 could not be calculated; the larvae were not old enough. Variance in otolith growth was significantly different between age classes; a log transformation successfully homogenized variances. Following calculation of the repeated-measures ANOVA, all pairwise comparisons of mean otolith growth were made between age classes using a Bonferroni correction.

To further examine phenotypic selection acting on larval size and growth rate, a nonparametric technique was used to determine relative survival functions. Schluter (1988) introduced the use of cubic splines to estimate the form of selection acting on a quantitative trait. Anderson (1995) modified this approach, making it applicable to cross-sectional data. This spline-based method makes no assumptions of the underlying fitness function, assumes the function is smoothly changing, and allows calculation of confidence intervals. The form of selection operating on otolith radii-at-increment 1 was calculated using 0–5 d old larvae as the "before-selection" age class and 5–10, 10–15 and 15–20 d old larvae as "after-selection" age classes. Similar
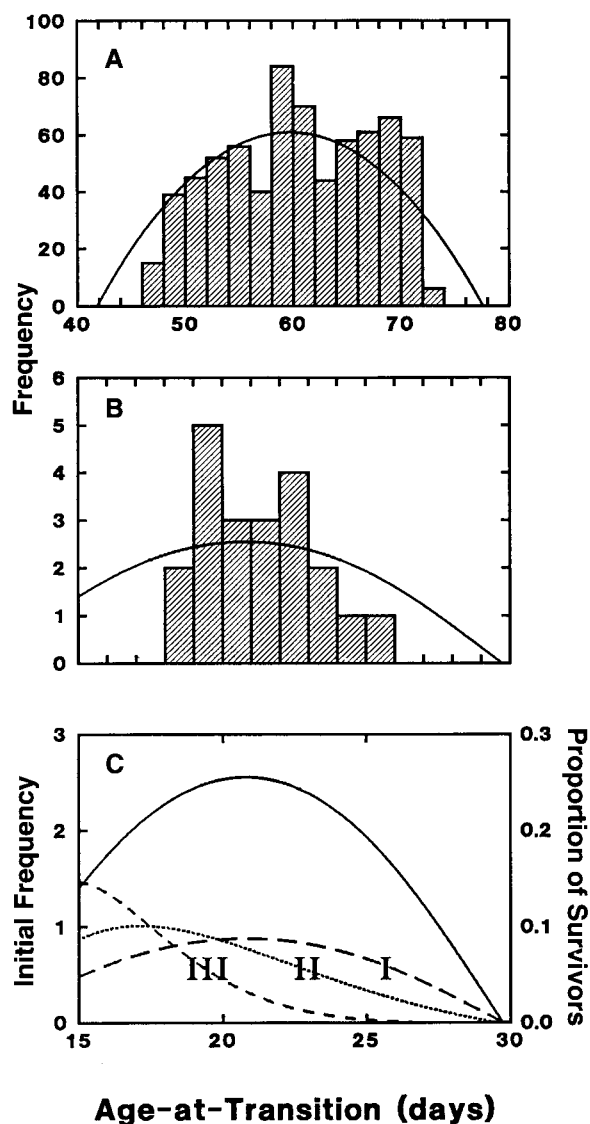
Age-at-Transition (days)

Fig. 4. (A) Frequency distribution of age-at-transition for laboratory-reared *Pseudopleuronectes americanus* (data from Fig. 1 in Chambers and Leggett 1987). A quadratic model (———) was used to represent this distribution (observed "before-selection" skewness = -0.116, observed "before-selection" kurtosis = -1.072; modeled "before-selection" skewness = 0.001, modeled "before-selection" kurtosis = -0.860). (B) Frequency distribution of age-at-transition for field-collected *Pomatomus saltatrix* derived from the numbers of otolith increments prior to secondary-growth-center formation (see Hare and Cowen 1994). In a cross-sectional analysis, these data represent the observed, "after-selection" distribution of the age-at-transition (observed "after-selection" skewness = 0.519, observed "after-selection" kurtosis = -0.409). Based on the data of Chambers and Leggett (1987) (see panel A), a quadratic model was used to represent the "before-selection" distribution (———) of age-at-transition in *Pomatomus saltatrix* (modeled "before-selection" skewness = 0.003, modeled "before-selection" kurtosis = -0.846). (C) A graphical representation of the analysis of the "stage-duration" mechanism. The assumed, "before-selection" distribution (———; from panel B) was subjected to different larval and juvenile mortality rates, resulting in modeled, "after-selection" distributions. Examples

analyses were conducted for the otolith radius-at-increments 5 (comparing 5–10 d old larvae with 10–15, 15–20, and >25 d old larvae), 10 (comparing 10–15 d old larvae with 15–20 and >25 d old larvae), 15 (comparing 15–20 d old larvae with larvae 20–25 and >25 d old larvae), and 20 (comparing 20–25 d old larvae with larvae >25 d old). The form of selection operating on otolith growth was similarly estimated. Otolith growth from increment 1 to 5 was analyzed using 5–10 d old larvae as the "before-selection" age class and 10–15, 15–20, and >25 d old larvae as "after-selection" age classes. Likewise, analyses were conducted for otolith growth between increments 5 and 10 (comparing 10–15 d old larvae with 15–20, 20–25, and >25 d old larvae), 10 and 15 (comparing 15–20 d old larvae with 20–25 and >25 d old larvae), and 15 and 20 (comparing 20–25 d old larvae with larvae >25 d old). Confidence intervals for the relative survival functions were estimated with 100 bootstrapped replicates (Anderson 1995).

Test of the "stage-duration" mechanism

A cross-sectional approach was also used to evaluate the prediction of the "stage-duration" mechanism (i.e., if there is a substantial decrease in mortality rate associated with the transition from larva to juvenile, then individuals that make the transition earlier will have a higher probability of survival). The "after-selection" distribution of age-at-transition was derived by enumerating the number of otolith increments preceding the formation of secondary growth centers on the sagittae of pelagic juvenile *Pomatomus saltatrix* (see Hare and Cowen 1994). A "before-selection" distribution of age-at-transition cannot be determined from field-collected fish, since individuals must become juveniles for age-at-transition to be measurable, and at this point, selection has already acted. Laboratory-reared fish, however, can be used to examine the distribution of age-at-transition in the absence of natural mortality, and such data are analogous to a "before-selection" distribution. Unfortunately, the distribution of age-at-transition for laboratory-reared fish has been derived for only a few species. The most thorough data is for *Pseudopleuronectes americanus* (Pisces: Pleuronectidae; Chambers and Leggett 1987; Fig. 4A) and the age-at-transition distribution was found to be platykurtic

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of three modeled, "afterselection" distributions (broken lines) are provided where the difference between larval and juvenile mortality was zero (model I), 0.15 (model II), and 0.45 (model III). The skewness (g_1) and kurtosis (g_2) of the modeled, "afterselection" distributions were then compared to the observed, "after-selection" distribution of age-at-transition for *P. saltatrix* to provide an estimate of the difference between larval and juvenile mortality experienced by *P. saltatrix* in the field (see panel B) (model I skewness = 0.003, model I kurtosis = -0.846; model II skewness = 0.477, model II kurtosis = -0.498; model III skewness = 1.132, model III kurtosis = 1.376).

(i.e., fewer measurements at the mean and the tails and more measurements intermediate when compared to a normal distribution; see Sokal and Rohlf 1981). To capture the platykurtic nature exhibited by these age-at-transition data, a quadratic equation was used as a model of the "before-selection" age-at-transition distribution for *P. saltatrix*. A quadratic equation was fit to the observed, "age-at-transition" data for *P. saltatrix* using the nonlinear estimation module of SYSTAT (Wilkinson 1990) (Fig. 4B).

Using the assumed, "before-selection" distribution of age-at-transition (i.e., the quadratic model shown in Fig. 4B), a selection model was developed that calculated "after-selection" distributions of age-at-transition using different values of larval and juvenile mortality. The skewness and kurtosis values of these modeled "after-selection" distributions were compared to the observed "after-selection" values (Fig. 4B) to estimate the difference between larval and juvenile mortality experienced by *Pomatomus saltatrix* in the field. Specifically, the selection model broke the "before-selection" distribution of age-at-transition into 20 age classes from 10 to 30 d. This discrete distribution was then subjected to the following exponential mortality model (see Peterson and Wroblewski 1984, McGurk 1986, 1993),

$$N_{Si} = N_{0i}(e^{-Z_L T_{Mi}})(e^{-Z_J(T_S - T_{Mi})})$$

where N_{Si} is the number of individuals surviving to 30 d in age-at-transition age class i, N_{0i} is the initial number of individuals in age class i as determined from the "before-selection," quadratic distribution, Z_L is the larval mortality rate, T_{Mi} is the age-at-transition for class i (from 10 to 30 d), Z_J is the juvenile mortality rate, and T_S is 30 d. The term $e^{-Z_L T_{Mi}}$ represents the proportion of N_{0i} that survives to the larval–juvenile transition and the term $e^{-Z_J(T_S - T_{Mi})}$ represents the proportion of individuals, which survived to the larval–juvenile transition, that survived to 30 d. A series of larval (Z_L) and juvenile (Z_J) mortality rates were used: 0.9, 0.75, 0.5, 0.25, 0.1, 0.05, 0.025, and 0 d^{-1}, with the restriction that larval mortality was either equal to or greater than juvenile mortality. The mean, variance, coefficient of variation, skewness, and kurtosis of the resulting modeled, "after-selection" distributions were then calculated (Sokal and Rohlf 1981). The "stage-duration" mechanism was evaluated by comparing the skewness and kurtosis of the modeled results with the values from the observed age-at-transition data to estimate the difference between larval and juvenile mortality for *P. saltatrix* in the field (Fig. 4C). Mean and variance were not compared because the quadratic model was initially fit to the observed data and thus the selection model gave no information on changes in these values.

Correlations among size, growth rate and development rate

Pearson correlation coefficients were calculated among measures of larval size, larval growth rate, and

the age at the larval–juvenile transition. Pearson correlations were calculated among the otolith radius at increments 1, 5, 10, 15, and 20 and among the otolith increment widths 1–5, 5–10, 10–15, and 15–20. Pearson correlations were also calculated between the increment widths and otolith radii-at-age listed above. Lastly, Pearson correlations were calculated between the age-at-transition and otolith size at increments 1, 5, 10, and 15 and otolith growth between increments 1–5, 5–10, 10–15, and 15–20.

RESULTS

"Bigger-is-better" and "growth-rate" mechanisms

Mean otolith increment radii increased with increasing larval age (Fig. 5A). All ANOVAs found a significant effect of age class on the radius to specific otolith increments except for increment 20 (increment 1, $F_S = 41.781$, $P < 0.001$; increment 5, $F_S = 30.394$, $P < 0.001$; increment 10, $F_S = 13.325$, $P < 0.001$; increment 15, $F_S = 9.488$, $P < 0.001$; increment 20, $F_S = 1.227$, $P > 0.05$). Pairwise comparisons of means typically found significant differences between nonadjoining age groups (e.g., 0–5 and 10–15) (Table 1). None of the ANOVAs found a significant effect of the independent counts for each individual nor any interaction between these counts and age class.

Mean otolith growth between specific increments increased with increasing larval age (Fig. 5B). All ANOVAs found a significant effect of age class except for otolith growth between increments 15 and 20 (increment 1 to 5, $F_S = 23.836$, $P < 0.001$; increment 5 to 10, $F_S = 9.493$, $P < 0.001$; increment 10 to 15, $F_S = 5.898$, $P < 0.01$; increment 15 to 20, $F_S = 0.285$, $P > 0.05$). Again, pairwise comparisons of means typically found significant differences between nonadjacent age groups (e.g., 5–10 and 15–20) (Table 1). None of the ANOVAs calculated for otolith growth found a significant effect of the independent counts for each individual nor any interaction between these counts and age class.

Estimation of the phenotypic selection functions found some examples of linear directional selection, but most functions were nonlinear (Fig. 6). The form of nonlinear functions varied from exponential, to asymptotic, to sigmoidal. In several cases, the estimated form of selection was complex with minor peaks at intermediate levels (e.g., otolith growth from increment 1 to 5 comparing 5–10 with 10–15 d old larvae, Fig. 6B). In two instances (otolith growth between increment 10 and 15 comparing 15–20 and >25 d old larvae and otolith growth between increment 15 and 20 comparing 20–25 with >25 d old larvae, Fig. 6B), there was evidence for stabilizing selection (i.e., intermediate values of otolith growth exhibited the highest probability of survival).

"Stage-duration" mechanism

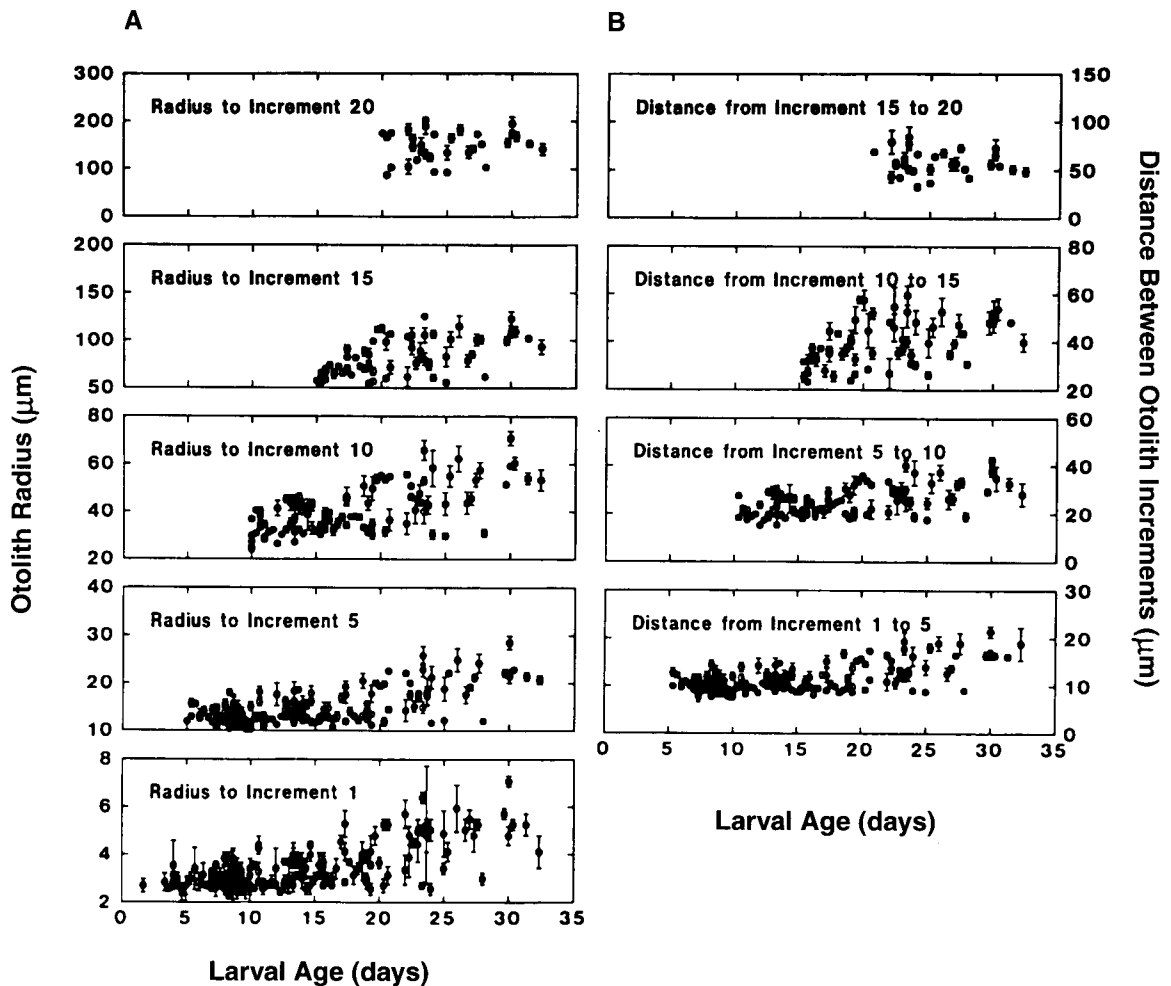The mean age at the larval–juvenile transition observed for *Pomatomus saltatrix* was 21.21 d (SD =

FIG. 5. (A) Otolith radius to increment 1, 5, 10, 15, and 20 and larval age of *Pomatomus saltatrix* larvae collected on the Middle Atlantic Bight shelf during the summer of 1988. Error bars represent the standard error of the mean based on three repeated measures of otolith radius. (B) Otolith growth between increments 1 and 5, 5 and 10, 10 and 15, and 15 and 20 and larval age of the same larvae depicted in panel A. Error bars represent the standard error of the mean based on three repeated measures of otolith radius.

3.83) and ranged from 18 to 25 d (Fig. 4B). The observed skewness ($g_1 = 0.519$) was significantly different than zero ($t_s = 2.380, P < 0.05$), while the observed kurtosis ($g_2 = -0.409$) was not ($t_s = 0.383, P > 0.05$). The quadratic model for the "before-selection" age-at-transition of *P. saltatrix* gave a skewness of 0.003 and a kurtosis of -0.846 (Fig. 4B).

The selection model found that the statistics of the modeled, "after-selection" age-at-transition distributions were functions of the difference in larval and juvenile mortality (Fig. 7). The selection model predicted that the mean and variance of the age-at-transition distribution would decrease as the difference in larval and juvenile mortality increased (Fig. 7A, B). The decrease in variance was initially less, but then greater than the decrease in the mean, resulting in an increasing then decreasing coefficient of variation (Fig. 7B). The selection model predicted increases in skew-

ness and kurtosis with an increasing difference between larval and juvenile mortality (Fig. 7C, D). Assuming the quadratic distribution (shown in Fig. 4B) represents the "before-selection" distribution of *Pomatomus saltatrix* age-at-transition, the observed, "after-selection" skewness (0.519) would indicate a difference in the instantaneous mortality rate of $\sim$0.15 d^{-1} between larvae and juveniles (Fig. 7C). Similarly, the observed, "after-selection" kurtosis (-0.409) would indicate a difference in instantaneous larval and juvenile mortality rate of $\sim$0.15 d^{-1} (Fig. 7D).

Correlation among larval size, growth rate, and development rate

All otolith increment radii and otolith growth measurements were positively correlated (Tables 2, and 3). An individual with a larger otolith at increment 1 was likely to have a larger otolith at increment 5, 10, 15,

TABLE 1. Results of pairwise contrasts of means of the otolith radius to specific increments (above diagonal) and otolith width between specific increments (below diagonal) for each age class: 0–5, 5–10, 10–15, 15–20, 20–25, >25 d. The F statistic for Wilks' λ (see Wilkinson 1990) is provided for each comparison. All comparisons were made, so a Bonferroni correction ([α = 0.05]/number of comparisons) was used to evaluate the significance of each contrast.

Otolith measurements (df; Bonferroni α)	Age class	Age class (d)				
		5–10	10–15	15–20	20–25	>25
A) Otolith radius to increment 1 (df = 3, 186; α = 0.003)	0–5	2.267	3.548	7.189*	21.905*	34.990*
	5–10	· · ·	2.132	6.861*	27.026*	45.823*
	10–15		· · ·	1.550	14.752*	29.830*
	15–20			· · ·	6.938*	19.681*
	20–25				· · ·	5.490*
	>25					
B) Otolith radius to increment 5 [above diagonal]; otolith width between increments 1 and 5 [below diagonal] (df = 3, 170; α = 0.005)	5–10	· · ·	2.382	2.919	19.585*	41.468*
	10–15	2.172	· · ·	0.461	9.417*	25.474*
	15–20	3.667	0.371	· · ·	6.682*	22.740*
	20–25	0.036	6.254*	5.476*	· · ·	7.198*
	>25	33.136*	19.791*	19.287*	5.600*	· · ·
C) Otolith radius to increment 10; otolith width between increments 5 and 10 (df = 3, 94; α = 0.008)	10–15		· · ·	0.362	5.463*	15.011*
	15–20		0.674	· · ·	3.083	11.142*
	20–25		4.852*	2.109	· · ·	3.117
	>25		10.246*	6.399*	1.587	· · ·
D) Otolith radius to increment 15: otolith width between increments 10 and 15 (df = 3, 56; α = 0.017)	15–20			· · ·	2.018	7.380*
	20–25			1.801	· · ·	2.056
	>25			4.387*	1.109	· · ·
E) Otolith radius to increment 20: otolith width between increments 15 and 20 (df = 3, 26; α = 0.05)	20–25				· · ·	0.684
	>25				0.965	· · ·

* $P < 0.05$.

and 20, as well as greater distances between otolith increments 1–5, 5–10, 10–15, and 15–20. Larvae with slower growing and smaller otoliths tended to make the larval–juvenile transition later compared to larvae with larger and faster growing otoliths, but the correlations were not significant (Table 3).

DISCUSSION

Larval size, growth rate, and survival

The otolith record of age, size, and development provides evidence that the survival of *Pomatomus saltatrix* larvae is linked to size and growth. Based on the idea that otolith size and growth are relative measures of larval size and growth (see Campana 1990, Hare and Cowen 1995), individuals that were larger at age 1 tended to be larger and faster growing throughout the larval stage (Tables 2 and 3), and owing to the correlative nature of size and growth, the "bigger-is-better" and "growth-rate" mechanisms of the "growth–mortality" hypothesis are synonymous for larval *P. sal-*

tatrix. Directional selection acting on size and growth was observed throughout the larval stage of *P. saltatrix* (Table 2, Fig. 6), indicating that no one point in the larval stage (e.g., the transition from yolk sac to feeding larvae) is "critical" to survival (see May 1974). Hence, the "bigger-is-better" and "growth-rate" mechanism apparently influenced survival during the entire larval stage.

While these results are consistent with the "growth–mortality" hypothesis, there are several factors that may have biased these analyses. First, all the fish examined may not have experienced the same prey and/or predator fields due to spatial and temporal variability in the environment and larval transport into and out of the sampling area. For example, while every effort was made to examine the same "cohort" of larvae (mean hatch date = 10 July, SD = 8.99 d; hatch date calculated as collection date − age), there were significant differences in hatch dates among some of the age groups (one-way ANOVA: F_s = 8.61, $P < 0.001$; Tukey post

A

Otolith Radius to Specific Increments (μm)

B

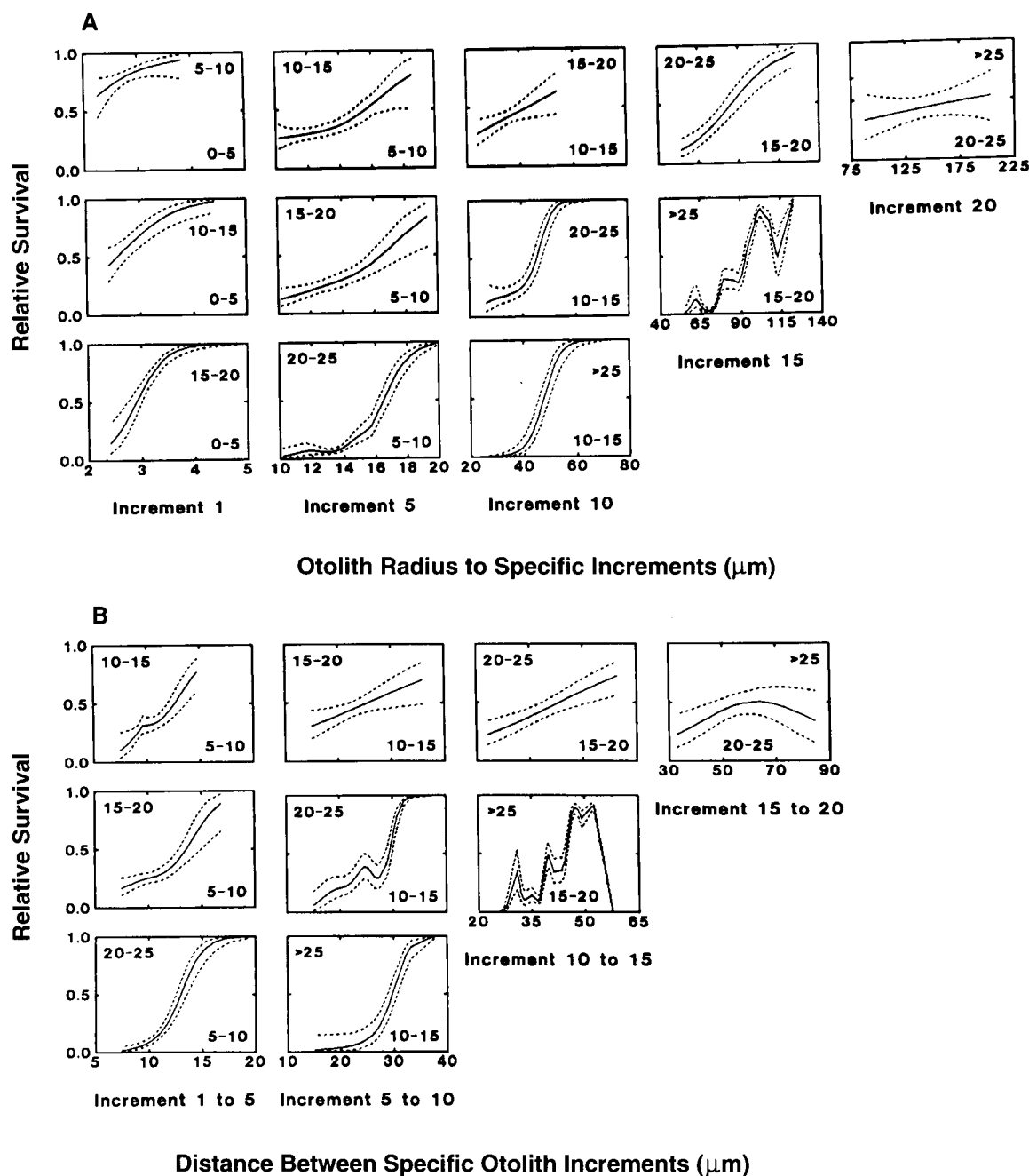**Distance Between Specific Otolith Increments (μm)**

FIG. 6. Relative survival functions based on otolith radius (A) and otolith growth (B). Functions were estimated using the cubic-spline technique of Schluter (1988) as modified by Anderson (1995). The age class used for the "before-selection" distribution is denoted in the bottom, right-hand corner of each plot, and the age class used for the "after-selection" distribution is denoted in the top, left-, or right-hand, corner of each plot (units are days). The 95% confidence intervals are based on 100 bootstrap replications.

hoc multiple comparison: hatch dates of 5–10 <10–15 and 15–20-d-old larvae and hatch dates of 10–15 >20–25 and >25-d-old larvae, pairwise mean differences = 9.86, 5.33, 9.10, and 10.50 d, respectively, $P < 0.05$) and thus, temporal variability in the environment could have influenced the results of this study. However, among the age groups for which hatch dates

were not significantly different, there were significant differences in otolith size and otolith growth (Table 1, Fig. 6). Yet, even for the fish with similar birthdates, the effect of alternative sources of variability cannot be fully excluded. Thus, spatial and temporal variability in the environment, as well as larval transport into and out of sampling areas present a general prob-
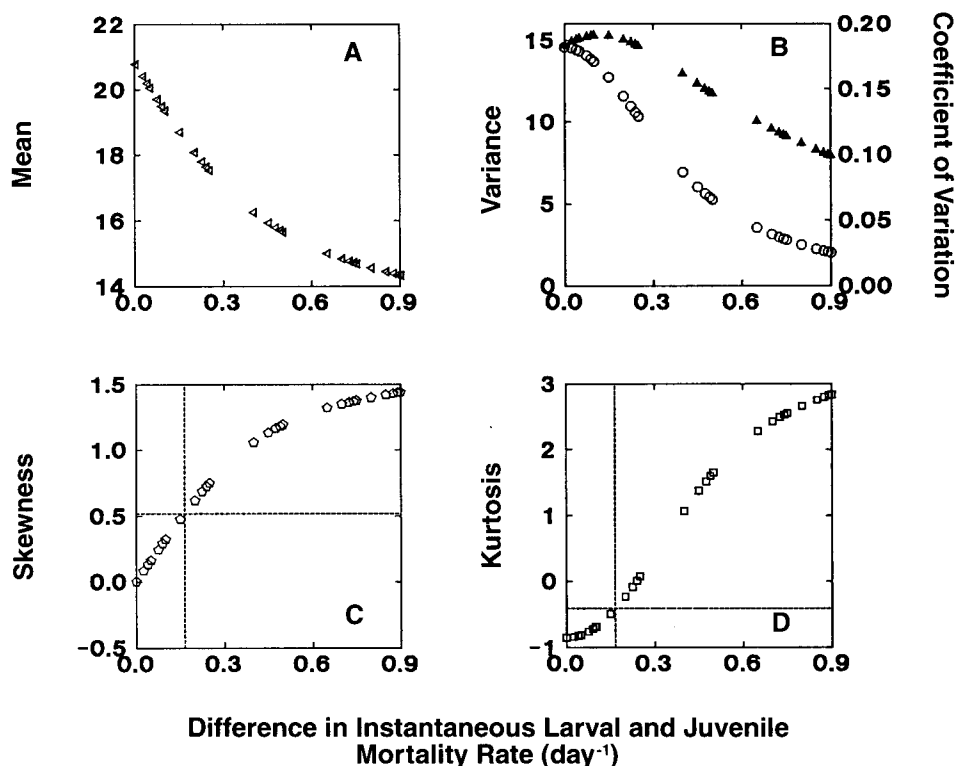
FIG. 7. Results of the selection model showing predicted changes in (A) mean, (B) variance (○) and coefficient of variation (▲), (C) skewness, and (D) kurtosis of age-at-transition under various combinations of larval and juvenile mortality. Horizontal lines indicate the observed skewness and kurtosis in the age-at-transition distribution in *Pomatomus saltatrix*. Vertical lines show where horizontal lines intersect with model results.

lem to the study of the "growth–mortality" hypothesis in the field, even when large areas are sampled as in this study (but see Tsukamoto et al. 1989). Future work should attempt to quantify the spatial areas occupied

TABLE 2. (A) Pearson correlation coefficients among otolith radii to specific increments for larval and pelagic proportion *Pomatomus saltatrix*. (B) Pearson correlation coefficients among otolith widths between specific increments for larval and pelagic juvenile *Pomatomus saltatrix*.

A)

Otolith radius at increment	Otolith radius at increment			
	5	10	15	20
1	0.888*	0.853*	0.792*	0.755*
5		0.956*	0.921*	0.918*
10			0.967*	0.944*
15				0.971*

B)

Growth between otolith increments	Growth between otolith increments		
	5 to 10	10 to 15	15 to 20
1 to 5	0.888*	0.832*	0.740*
5 to 10		0.878*	0.776*
10 to 15			0.792*

* $P < 0.05$.

by surviving larvae in relation to the "growth–mortality" hypothesis, thereby elucidating the role of spatial variability in affecting larval survival.

Another factor that may have influenced the results of this study is error in the otolith radii measurements. To account for measurement errors, repeated blind measurements of otolith increment radii were made and no significant effects of the repeated measures nor interactions with age classes were detected. A potential measurement bias is systematic aging errors, whereby early increments are missed in older fish, resulting in larger otolith radii-at-increment and underestimation of true age. A comparison of larval length and estimated ages from this study with a study of the estuarine juvenile stage (50–100 d) does not support this possible explanation (see Fig. 2 in Juanes et al. 1996). Thus, measurement errors do not appear to have influenced the results of this study.

A potential concern is that fish with larger and faster growing otoliths were not observed as younger members of the cohort (Fig. 5). A similar result was found by Tsukamoto et al. (1989) in a study of size-dependent mortality in juvenile *Pagrus major* (Pisces: Sparidae). The otoliths of 267 000 *P. major* were marked with tetracycline and the fish were released into the wild. Fish collected 6 d after release ($n = 500$) had a mean

TABLE 3. (A) Pearson correlation coefficients between otolith radii to specific increments and otolith widths between specific increments for larval and pelagic juvenile *Pomatomus saltatrix*. (B) Pearson correlation coefficients between age at the larval–juvenile transition and otolith radius to specific increments and otolith width between specific increments for *Pomatomus saltatrix*. The youngest observed age-at-transition was 18 d, and thus, correlations between age-at-transition and growth between otolith increments 15 and 20 and otolith radius at increment 20 were not calculated.

A)

Growth between otolith increments	Otolith radius at increment				
	1	5	10	15	20
1 to 5	0.799*	0.982*	0.939*	0.911*	0.895*
5 to 10	0.783*	0.872*	0.975*	0.961*	0.940*
10 to 15	0.660*	0.797*	0.856*	0.960*	0.934*
15 to 20	0.663*	0.774*	0.769*	0.814*	0.927*

B)

	Otolith radius at increment				Growth between otolith increments		
	1	5	10	15	1 to 5	5 to 10	10 to 15
Correlation with age at transition	−0.071	−0.148	−0.175	−0.301	−0.112	−0.205	−0.408

* $P < 0.05$.

otolith radius to the tetracycline mark of 216.5 μm, while fish collected 86 d after release ($n = 549$) had a mean otolith radius to the mark of 238.8 μm. Approximately 15% of the fish collected at 86 d had otolith radii to the mark that were greater than the maximum observed at 6 d. Similar results (i.e., larger otoliths found in survivors compared to otoliths observed in younger fish) have been found in several other studies (freshwater, Post and Prankevicius 1987, West and Larkin 1987; marine, DeVries et al. 1990, Meekan and Fortier 1996). This observation can be explained by the "wastage" (sensu Thorson 1950) experienced by planktonic larvae. Survival to the juvenile stage is on the order of 1–0.001% (Houde 1987). If mortality is size- and/or growth-rate selective, then a huge number of individuals would need to be examined (~100 000 individuals) to observe survivors as young larvae. Given the sample sizes typical of most larval fish studies (hundreds to thousands), one should not expect that the older, surviving individuals will be encountered as younger larvae. Further, as discussed above, it is possible that some of the individuals in this study did not experience the same environment, thereby contributing to the presence of older individuals with larger and faster growing otoliths.

Another potential concern is that the variance of otolith size and growth often increased with increasing age. The traditional view of directional selection holds that the mean of the trait will change and the variance will generally decrease (see Endler 1986), yet the outcome of directional selection on variance is dependent on the specific form of selection (Fig. 2). In the present study, nonlinear and linear survival functions were found (Fig. 6) and thus, increases in variance should

be expected. In fact, we found examples of both increasing and decreasing variance following selection. In all the examples of selection shown in Fig. 2, the coefficient of variation (CV) decreases, but in the otolith size and growth data, there are instances where the CV increases with increasing age. These findings suggest that further modeling studies of the effect of nonlinear directional selection on quantitative traits are needed prior to in-depth analyses of changes in variance and CV. Overall, the observed data agree with the expectations of the "bigger-is-better" and "growth-rate" mechanisms of the "growth–mortality" hypothesis, though there are indications (e.g., changes in variance and CV) that other factors (e.g., larval transport, environmental variability, the "stage-duration" mechanism [see below]) may be involved in determining the appearance of older fish with larger and faster growing otoliths.

In ecosystems with a few dominant predators (see Paine 1966, 1980), the probability of mortality may not be a constantly decreasing function of larval size or growth rate. Litvak and Leggett (1992) and Pepin et al. (1992) have found that in some instances, individual predators select larval prey that are larger-at-age. There may be "keystone" predators in pelagic systems, for example, gelatinous zooplankton (see Aria 1988, Govoni and Olney 1991), and the role of such predators in influencing size- and growth-dependent survival should not be ignored. However, pelagic ecosystems generally consist of a myriad of predators of various sizes. Even if individual predators are choosing prey items at the upper size range of their prey field, the number of predators decreases as predator size increases (Sheldon et al. 1972, 1973, Platt and Denman 1978).

Thus, larger and faster growing larvae will be less susceptible to predation by the entire predator field in a typically complex, pelagic system but not necessarily so in pelagic systems dominated by a few predators.

Larval–juvenile transition and survival

The otolith record of larval size, growth, and development indicates that the "stage-duration" mechanism of the "growth–mortality" hypothesis can act independently of the "bigger-is-better" and "growth-rate" mechanisms. Otolith size and growth were not significantly correlated to the age at the larval–juvenile transition in *Pomatomus saltatrix*. Recent work has suggested that growth and development rate may not be synonymous (e.g., McCormick 1993, 1994). Slower growing, smaller individuals that make the larval-juvenile transition earlier could potentially have a higher probability of survival compared to larger, faster growing individuals that make the larval–juvenile transition later.

Support for the "stage-duration" mechanism was provided by the cross-sectional analysis of the age-at-transition distribution, but conclusions are limited by assumptions. A modeled, "before-selection" distribution should be determined for the species under study; this would allow all characteristics (i.e., mean, variance, skewness, kurtosis) of the age-at-transition distribution to be evaluated in terms of the predictions of the "stage-duration" mechanism. However, assuming the platykurtic distribution of age-at-transition of laboratory-reared *Pseudopleuronectes americanus* can be generalized to *Pomatomus saltatrix* (an assumption worthy of further investigation), comparison of skewness and kurtosis values from the modeled, "after-selection" distributions with those from the observed, "after-selection" distribution suggests that the difference between larval and juvenile mortality rate in *Pomatomus saltatrix* is ~0.15 d^{-1}. Houde (1987) reported the instantaneous mortlity rate for the larvae and juveniles of five species. The difference in larval and juvenile mortality rate averaged 0.12 d^{-1} for all species examined and 0.16 d^{-1} for the three warmer water species. The similarity between Houde's (1987) values and that derived from the comparison of the observed age-at-transition distribution with the results of the selection model is intriguing and provides support for the idea that there is a decrease in mortality associated with the larval–juvenile transition and, by extension, that the duration of the larval stage may regulate, to some degree, the survival of marine fishes.

An increase in the skewness of the age-at-transition distribution, as seen in the selection model, has also been observed in species that delay metamorphosis, which is the ability of individuals to prolong their larval stage while retaining the capacity to make the larval–juvenile transition (see Pechenik 1986, Cowen 1991). If a "before-selection" and "after-selection" age-at-transition distribution can be obtained from one

species, then the predictions of the "stage-duration" mechanism can be separated from delayed metamorphosis. Under the "stage-duration" mechanism, the "after-selection" mean and variance in age-at-transition should be lower than observed in a "before-selection," "nondelaying" distribution (Fig. 7). If wild-caught larvae were delaying their metamorphosis and the "stage-duration" mechanism was not operating, the mean and variance of the observed distribution would be higher than that found in a "before-selection," "nondelaying" distribution. Further use of cross-sectional analyses of the age at the larval–juvenile transition will lead to further insights into ecological aspects of the timing of the larval–juvenile transition and the role of development rate in affecting larval survival.

Maintenance of phenotypic variability under directional selection

If larger and faster growing larvae have an advantage in terms of feeding, avoiding predation, and resisting starvation (see reviews by Hunter 1981, Miller et al. 1988, Bailey and Houde 1989), why do marine fishes and benthic invertebrates produce small offspring? This question has received much attention (e.g., Elgar 1990, Strathmann 1993, Winemiller and Rose 1993), but the related question of what maintains phenotypic variation in larval size and growth has not (see Meekan and Fortier [1996] for a similar discussion). There are at least three, nonexclusive explanations for the maintenance of low and/or variable size-at-age and growth rate under the directional selection observed in this study. One explanation involves the genetic basis for the trait and for variation in the trait. Heritabilities of fish life history traits have been found to be significantly positive in some cases, but not in others (e.g., Stearns 1983, Chambers et al. 1989, Snyder and Dingle 1989). If larval size and growth are not genetically based, then evolution of these traits would not be expected. Alternatively, if the positive correlation between the traits and fitness is exclusively due to a nonheritable, environmental component, then even a heritable trait will not evolve (e.g., Price et al. 1988, Alatalo et al. 1990). Environmental factors are known to affect egg size, egg quality, size at hatching, and larval growth (see Hempel 1979, Hunter 1981, Chambers and Leggett 1996) and thus, nonheritability or correlation between environmental variation and fitness could explain the maintenance of small offspring size and variation in offspring size under directional phenotypic selection.

It is also possible that selection acting on other ontogenetic stages counteracts directional selection acting during the larval stage. This may be indicated by the apparent stabilizing selection on larval growth at the older ages (Fig. 6). One scenario is that individuals that grow and develop faster are at a disadvantage after the larval–juvenile transition because function of partic-

ular systems (e.g., sensory; see McCormick 1993) is dependent on development time (see Galis et al. 1994). Meristic characters (e.g., fin rays, vertebrae) are thought to be negatively related to development rate (Tåning 1952, Barlow 1961) and higher meristics may be selected for after the larval stage (see Swain 1992a, b). Additionally, compensatory growth, whereby growth rates in the larval and juvenile stage are negatively correlated (Bertram et al. 1993), would decrease the probability of survival during the juvenile stage for fast-growing larvae. Finally, while the observations here find that larger offspring, presumably resulting from larger eggs (Hempel 1979, Hunter 1981, Miller et al. 1988), have a higher probability of survival, natural selection acting on the spawning female may favor more, smaller eggs (see Winemiller and Rose 1993). There are other potential scenarios, but the point is that selection during other portions of the life history may counter the directional selection observed here and, thus, act to maintain phenotypic variability in larval size and growth.

A final explanation for the maintenance of phenotypic variation in larval size and growth is that selection operates on a trait correlated with growth rate and size. Significant correlations were found between size and growth (Tables 2 and 3) and in general, the early life history traits of individual larvae are highly correlated (Chambers et al. 1988, 1989). The results of phenotypic selection acting on one trait would be observed as selection acting on other correlated traits (Lande 1979, Riska 1989). For example, larval growth may be negatively related to larval activity owing to metabolic constraints (Wieser et al. 1988, Wieser and Medgyesy 1990). If both greater activity and higher growth rate are under directional selection, then the combined result would maintain growth rates that appear suboptimal (see West and Larkin 1987, Mosegaard 1990). Another complicating factor is that the direction of selection on correlated traits may change over the larval period, as exemplified by vertebral characters in larval *Gasterosteus aculeatus* (Swain 1992a, b). Without understanding the true targets of selection, one cannot predict the evolutionary response of one trait to phenotypic selection.

Ecological implications of size-selective and growth-rate-selective mortality

A major research goal in marine ecology is to understand the processes that cause variation in recruitment. Hjort (1914) hypothesized that growth-related processes acting during the larval stage influence recruitment to marine fish populations. The present study and others (Post and Prankevicius 1987, West and Larkin 1987, Tsukamoto et al. 1989, DeVries et al. 1990, Meekan and Fortier 1996) indicate that within a cohort of larvae, larger and faster growing individuals have a higher probability of survival. Based on such size-selective mortality, modeling studies have found that faster growing cohorts will exhibit higher survival and recruitment compared to slower growing cohorts (a between-cohort comparison; DeAngelis et al. 1993, Rice et al. 1993). The question that must now be answered is do faster growing cohorts of larvae exhibit higher recruitment compared to slower growing cohorts of larvae?

The maternal contribution via egg size and egg quality may also be a significant factor in determining larval survival, given its apparent link to larval size and growth (Figs. 5 and 6). Egg size varies across many scales: within a spawning season egg size typically decreases as the season progresses; larger females often produce larger eggs; environmental factors (e.g., salinity, temperature) affect egg size (see Hempel 1979, Chambers and Leggett 1996). While the influence of egg size and quality on larval fish survival has been examined theoretically (Ware 1975), within-cohort variation in survival has yet to be directly linked with variation in egg size or other measures of maternal contribution.

Physical processes add another confounding layer in evaluating the importance of biological processes in determining larval survival. During planktonic stages, larvae may move through various water masses, resulting in changes in the prey and predator fields. Water mass characteristics (e.g., temperature) may also affect egg size as described above as well as influence larval vital rates (e.g., metabolic, growth). These physically caused, biological changes may affect cohort survival, but have yet to be fully assessed. In addition, some species require directed transport from spawning grounds to appropriate juvenile habitat (e.g., Epifanio et al. 1989, Hare and Cowen 1996) and thus, transport processes may influence larval survival, apart from the growth–mortality context.

In pelagic ecosystems, both biological and physical processes act on larval survival and shape the patterns of recruitment to adult populations. Biological processes include the size, growth, and developmental interactions with mortality discussed here, as well as biologically caused changes in the prey and predator fields and differences in maternal contribution to the eggs. Physical processes move larvae to different water masses, thereby exposing them to different prey and predator communities. Hydrographic properties may also influence egg characteristics and larval vital rates. Finally, physical transport may move larvae to or from areas favorable to juvenile survival. The relative degree to which these processes act varies among species and within species among systems. Different species have different life histories, different susceptibilities to starvation and predation, and different growth and ontogenetic trajectories. Within a given system (e.g., the continental shelf of the Middle Atlantic Bight), larvae of all species are faced with the same overall prey, predator, and transport characteristics, yet embedded within a system are different water masses and seasonal

changes. If we can couple the parameters of the size structure of a pelagic ecosystem with an understanding of the species-specific maternal contribution to offspring and the dual nature of physical processes, then the recruitment dynamics of various species, fish and invertebrates, can be integrated within one, system-level framework.

LITERATURE CITED

Alatalo, R. V., L. Gustafsson, and A. Lundberg. 1990. Phenotypic selection on heritable size traits: environmental variance and genetic response. American Naturalist 135:464–471.

Anderson, C. S. 1995. Calculating size-dependent relative survival from samples taken before and after selection. Pages 455–466 in D. H. Secor, J. M. Dean, and S. E. Campana, editors. Recent developments in fish otolith research. Belle W. Baruch Library in Marine Sciences Number 19. University of South Carolina Press, Columbia, South Carolina, USA.

Anderson, J. T. 1988. A review of size dependent survival during pre-recruit stages of fishes in relation to recruitment. Journal of Northwest Atlantic Fishery Science 8:55–66.

Arai, M. N. 1988. Interactions of fish and pelagic coelenterates. Canadian Journal of Zoology 66:1913–1927.

Bailey, K. M., and E. D. Houde. 1989. Predation on eggs and larvae of marine fishes and the recruitment problem. Advances in Marine Biology 25:1–83.

Barlow, G. W. 1961. Causes and significance of morphological variation in fishes. Systematic Zoology 10:105–117.

Bertram, D. F., R. C. Chambers, and W. C. Leggett. 1993. Negative correlations between larval and juvenile growth rates in winter flounder: implications of compensatory growth for variation in size-at-age. Marine Ecology Progress Series 96:209–215.

Brown, A. L., and K. M. Bailey. 1992. Otolith analysis of juvenile walleye pollock Theragra chalcogramma from the western Gulf of Alaska. Marine Biology 112:23–30.

Campana, S. E. 1990. How reliable are growth back-calculations based on otoliths. Canadian Journal of Fisheries and Aquatic Sciences 47:2219–2227.

Campana, S. E., and E. Mokness. 1991. Accuracy and precision of age and hatch date estimation from otolith microstructure examination. International Council for the Exploration of the Sea Journal of Marine Sciences 48:303–316.

Campana, S. E., and J. D. Neilson. 1985. Microstructure of fish otoliths. Canadian Journal of Fisheries and Aquatic Sciences 42:1014–1032.

Castro, L. R., and R. K. Cowen. 1991. Environmental factors affecting the early life history of bay anchovy, Anchoa mitchilli in Great South Bay, New York. Marine Ecology Progress Series 76:235–247.

Chambers, R. C., and W. C. Leggett. 1987. Size and age at metamorphosis in marine fishes: an analysis of laboratory-reared winter flounder (Pseudopleuronectes americanus) with a review of variation in other species. Canadian Journal of Fisheries and Aquatic Sciences 44:1936–1947.

Chambers, R. C., and W. C. Leggett. 1996. Maternal influences on variation in egg sizes in temperate marine fishes. American Zoologist 36:180–196.

Chambers, R. C., W. C. Leggett, and J. A. Brown. 1988. Variation in and among early life history traits of laboratory reared winter flounder Pseudopleuronects americanus. Canadian Journal of Fisheries and Aquatic Sciences 47:1–15.

Chambers, R. C., W. C. Leggett, and J. A. Brown. 1989. Egg size, female effects, and the correlations between early life history traits of capelin, Mallotus villosus: an appraisal at the individual level. United States National Marine Fisheries Service Fishery Bulletin 87:515–523.

Cock, A. G. 1966. Genetical aspects of metrical growth and form in animals. Quarterly Review of Biology 41:131–190.

Conover, R. J. 1978. Feeding interactions in the pelagic zone. Conseil International pour l'Exploration de la Mer 173:66–76.

Cowen, R. K. 1991. Variation in the planktonic larval duration of the temperate wrasse Semicossyphus pulcher. Marine Ecology Progress Series 69:9–15.

Cowen, R. K., J. A. Hare, and M. P. Fahay. 1993. Beyond hydrography: can physical processes explain larval fish assemblages within the Middle Atlantic Bight? Bulletin of Marine Science 53:567–587.

Crecco, V., and T. Savoy. 1987. Effects of climate and density dependent factors on intra-annual mortality of larval American shad. American Fisheries Society Symposium 2:69–81.

DeAngelis, D. L., K. A. Rose, L. B. Crowder, E. A. Marschall, and D. Lika. 1993. Fish cohort dynamics: application of complementary modeling approaches. American Naturalist 142:604–622.

DeVries, D. A., C. B. Grimes, K. L. Lang, and D. B. White. 1990. Age and growth of king and Spanish mackerel larvae and juveniles from the Gulf of Mexico and U.S. South Atlantic Bight. Environmental Biology of Fishes 29:135–143.

Elgar, M. A. 1990. Evolutionary comprimise between a few large and many small eggs: comparitive evidence in teleost fish. Oikos 59:283–287.

Endler, J. A. 1986. Natural selection in the wild. Princeton University Press, Princeton, New Jersey, USA.

Epifanio, C. E., A. K. Masse, and R. W. Garvine. 1989. Transport of blue crab larvae by surface currents off Delaware Bay, USA. Marine Ecology Progress Series 54:35–41.

Gaines, S. D., and J. Roughgarden. 1985. Larval settlement rate: a leading determinant of structure in an ecological community of the marine intertidal zone. Proceedings of the National Academy of Sciences (USA) 82:3707–3711.

Gaines, S. D., and J. Roughgarden. 1987. Fish predation in offshore kelp forests affect recruitment to intertidal barnacle populations. Science 235:479–481.

Galis, F., A. Terlouw, and J. M. Osse. 1994. The relation between morphology and behaviour during ontogenetic and evolutionary changes. Journal of Fish Biology 45:13–26.

Govoni, J. J., and J. E. Olney. 1991. Potential predation on fish eggs by the lobate ctenophore Mnemiopsis leidyi within and outside the Chesapeake Bay plume. Fisheries Bulletin 89:181–186.

Graham, J. J., and D. W. Townsend. 1985. Mortality, growth,

and transport of larval Atlantic herring *Clupea harengus* in Maine coastal waters. Transactions of the American Fisheries Society **114**:490–498.

Hare, J. A., and R. K. Cowen. 1991. Expatriation of *Xyrichtys novacula* (Pisces: Labridae) larvae: evidence of rapid cross-slope exchange. Journal of Marine Research **49**:801–823.

Hare, J. A., and R. K. Cowen. 1994. Ontogeny and otolith microstructure of bluefish *Pomatomus saltatrix* (Pisces: Pomatomidae). Marine Biology **118**:541–550.

Hare, J. A., and R. K. Cowen. 1995. The effect of age, growth rate and ontogeny on the relationship between otolith and somatic size in bluefish, *Pomatomus saltatrix,* and the implications for the backcalculation of size in the early life history of fishes. Canadian Journal of Fisheries and Aquatic Sciences **52**:1909–1922.

Hare, J. A., and R. K. Cowen. 1996. Transport mechanisms of bluefish *(Pomatomus saltatrix)* larvae from South Atlantic Bight spawning grounds to Middle Atlantic Bight nursery habitats. Limnology and Oceanography **41**:1264–1280.

Hempel, G. 1979. Early life history of marine fish: the egg stage. University of Washington Press, Seattle, Washington, USA.

Hjort, J. 1914. Fluctuations in the great fisheries of Northern Europe. Conseil International pour l'Exploration de la Mer **20**:1–228.

Hoenig, J. M., P. Pepin, and W. D. Lawing. 1990. Estimating relative survival rate for two groups of larval fishes from field data: do older larvae survive better than young? United States National Marine Fisheries Service Fishery Bulletin **88**:485–491.

Houde, E. D. 1987. Fish early life dynamics and recruitment varaibility. American Fisheries Society Symposium **2**:17–29.

———. 1989. Comparative growth, mortality, and energetics of marine fish larvae: temperature and implied latitudinal effects. United States National Marine Fisheries Service Fishery Bulletin **87**:471–495.

Hunter, J. R. 1981. Feeding ecology and predation of marine fish larvae. Pages 34–77 *in* R. Lasker, editor. Marine fish larvae: morphology, ecology, and relation to fisheries. Washington Sea Grant Program, University of Washington, Seattle, Washington, USA.

Jones, G. P. 1991. Postrecruitment processes in the ecology of coral reef fish populations: a multifactorial persepctive. Pages 294–328 *in* P. F. Sale, editor. The ecology of fishes on coral reefs. Academic Press, New York, New York, USA.

Juanes, F., J. A. Hare, and A. T. Miskiewicz. 1996. Comparing early life history strategies of *Pomatomus saltatrix*: a global approach. Marine Freshwater Research **47**:365–379.

Laidig, T. E., S. Ralston, and J. R. Bence. 1991. Dynamics of growth in the early life history of shortbelly rockfish *Sebastes jordani*. United States National Marine Fisheries Service Fishery Bulletin **89**:611–621.

Lande, R. 1979. Quantitative genetic analysis of multivariate evolution, applied to brain:body size allometry. Evolution **33**:402–416.

Lande, R., and S. J. Arnold. 1983. The measurement of selection on correlated characters. Evolution **37**:1210–1226.

Lasker, R. 1978. The relation between oceanographic conditions and larval anchovy food in the California Current: identification of factors contributing to recruitment failure. Conseil International pour l'Exploration de la Mer **173**:212–230.

Leggett, W. C., and E. DeBlois. 1994. Recruitment in marine fishes: is it regulated by starvation and predation in the egg and larval stage. Netherlands Journal of Sea Research **32**:119–134.

Leis, J. 1991. The pelagic stages of reff fishes: the larval biology of coral reef fishes. Pages 183–230 *in* P. F. Sale, editor. The ecology of fishes on coral reefs. Academic Press, San Diego, California, USA.

Litvak, M. K., and W. C. Leggett. 1992. Age and size-selective predation on larval fishes: the bigger-is-better hypothesis revisited. Marine Ecology Progress Series **81**:13–24.

May, R. C. 1974. Larval mortality in marine fishes and the critical period cocept. *In* J. H. S. Blaxter, editor. The early life history of fish. Springer-Verlag, Berlin, Germany.

McCormick, M. I. 1993. Development and changes at settlement in the barbel structure of the reef fish, *Upeneus tragula*. Environmental Biology of Fishes **37**:269–282.

———. 1994. Variability in age and size at settlement of the tropical goatfish *Upeneus tragula* (Mullidae) in the northern Great Barrier Reef lagoons. Marine Ecology Progress Series **103**:1–15.

McGurk, M. D. 1986. Natural mortality of marine pelagic fish eggs and larvae: role of spatial patchiness. Marine Ecology Progress Series **34**:227–242.

———. 1993. Allometry of herring mortality. Transactions of the American Fisheries Society **122**:1035–1042.

Meekan, M., and L. Fortier. 1996. Selection for fast growth during the larval life of Atlantic cod *Gadus morhua* on the Scotian shelf. Marine Ecology Progress Series **137**:25–37.

Methot, R. D. 1983. Seasonal variation in survival of larval *Engraulis mordax* estimated from the age distribution of juveniles. United States National Marine Fisheries Service Fishery Bulletin **81**:741–750.

Miller, T. J., L. B. Crowder, J. A. Rice, and E. A. Marschall. 1988. Larval size and recruitment mechanisms in fishes: toward a conceptual framework. Canadian Journal of Fisheries and Aquatic Sciences **45**:1657–1670.

Morse, W. W. 1989. Catchability, growth, and mortality of larval fishes. United States National Marine Fisheries Service Fishery Bulletin **87**:417–446.

Mosegaard, H. 1990. What is reflected by otolith size at emergence?—a reevaluation of the results in West and Larkin (1987). Canadian Journal of Fisheries and Aquatic Sciences **47**:225–228.

Nyman, R. M. 1987. The relation between oceanic spawning season and recruitment of juvenile bluefish, *Pomatomus saltatrix,* to New York waters. Master's thesis, State University of New York, Stony Brook, New York, USA

Nyman, R. M., and D. O. Conover. 1988. The relation between spawning season and the recruitment of young-of-the-year bluefish, *Pomatomus saltatrix,* to New York. United States National Marine Fisheries Service Fishery Bulletin **86**:237–250.

Paine, R. T. 1966. Food web complexity and species diversity. American Naturalist **100**:65–75.

———. 1980. Food webs: linkage, interaction strength and community infrastructure. Journal of Animal Ecology **49**:667–685.

Paulay, G., L. Boring, and R. R. Strathmann. 1985. Food limited growth and development of larvae: experiments with natural sea water. Journal of Experimental Marine Biology and Ecology **93**:1–10.

Pechenik, J. A. 1986. Field evidence for delayed metamorphosis of larval gastropds: *Crepidula plana* Say, *C. fornicata* (L.), and *Bittium alternatum* (Say). Journal of Experimental and Marine Biology and Ecology **97**:313–319.

Pepin, P. 1991. Effect of temperature and size on development, mortality, and survival rates of the pelagic early life history stages of marine fish. Canadian Journal of Fisheries and Aquatic Science **48**:503–518.

Pepin, P., T. H. Shears, and Y. de Lafontaine, 1992. Significance of body size to the interaction between larval fish

(*Mallotus villosus*) and a vertebrate predator (*Gasterosteus aculeatus*). Marine Ecology Progress Series **81**:1–12.

Peterson, I., and J. S. Wroblewski. 1984. Mortality rate of fishes in the pelagic ecosystem. Canadian Journal of Fisheries and Aquatic Sciences **41**:1117–1120.

Platt, T., and K. Denman. 1978. The structure of pelagic marine ecosystems. Conseil International pour l'Exploration de la Mer **173**:60–65.

Post, J. R., and A. B. Prankevicius. 1987. Size-selective mortality in young-of-the-year yellow perch (*Perca flavescens*): evidence from otolith microstructure. Canadian Journal of Fisheries and Aquatic Sciences **44**:1840–1847.

Price, T., M. Kirkpatrick, and S. J. Arnold. 1988. Directional selection and the evolution of breeding date in birds. Science **240**:798–799.

Purcell, J. E. 1989. Predation on fish larvae and eggs by the hydromedusa (*Aequorea victoria*) at a herring spawning ground in British Columbia. Canadian Journal of Fisheries and Aquatic Sciences **46**:1415–1427.

Rice, J. A., L. B. Crowder, and M. E. Holey. 1987. Exploration of mechanisms regulating larval survival in Lake Michigan bloater: a recruitment analysis based on characsitics of indiviudal larvae. Transactions of the American Fisheries Society **116**:703–718.

Rice, J. A., T. J. Miller, L. B. Crowder, E. A. Marschall, A. S. Trebitz, and D. L. DeAngelis. 1993. Growth rate variation and larval survival: inferences from an individual-based, size-dependent predation model. Canadian Journal of Fisheries and Aquatic Sciences **50**:133–142.

Riska, B. 1989. Composite traits, selection response and evolution. Evolution **43**:1172–1191.

Rothschild, B. J. 1986. Dynamics of marine fish populations. Harvard University Press, Cambridge, Massachusetts, USA.

Schluter, D. 1988. Estimating the form of natural selection on a quantitative trait. Evolution **42**:849–861.

Sheldon, R. W., A. Prakash, and W. H. Sutcliffe. 1972. The size distribution of particles in the ocean. Limnology and Oceanography **17**:327–340.

Sheldon, R. W., W. H. Sutcliffe, and A. Prakash. 1973. The production of particles in the surface waters of the ocean with particular reference to the Sargasso Sea. Limnology and Oceanography **18**:719–733.

Shepherd, J. G., and D. H. Cushing. 1980. A mechanism for density-dependent survival of larval fish as the basis of a stock-recruitment relationship. Journal du Conseil **40**:67–75.

Smith, W., P. Berrien, and T. Potthoff. 1994. Spawning patterns of bluefish, *Pomatomus saltatrix*, in the Northeast Continental Shelf Ecosystem. Bulletin of Marine Science **54**:8–16.

Snyder, R. J., and H. Dingle. 1989. Adaptive, genetically based differences in life history between estuary and fresh-

water threespine sticklebacks (*Gasterosteus aculeatus* L.). Canadian Journal of Zoology **67**:2448–2454.

Sokal, R. R., and F. J. Rohlf. 1981. Biometry. Second edition. W. H. Freeman, New York, New York, USA.

Stearns, S. C. 1983. The evolution of life-history traits in mosquitofish since their introduction to Hawaii in 1905: rates of evolution, heritabilities, and developmental plasticity. American Zoologist **23**:65–75.

Stevenson, D. K., and S. E. Campana. 1992. Otolith microstructure examination and analysis. Canadian Specical Publication in Fisheries and Aquatic Sciences **117**.

Strathmann, R. R. 1993. Hypotheses on the origin of marine larvae. Annual Review of Ecology and Systematics **24**:89–117.

Swain, D. P. 1992*a*. The functional basis of natural selection for vertebral traits of larvae in the stickleback *Gasterosteus aculaetus*. Evolution **46**:987–997.

———. 1992*b*. Selective predation for vertebral number phenotype in *Gasterosteus aculaetus*: reversal in the direction of selection at different larval size. Evolution **46**:998–1013.

Tåning, A. V. 1952. Experimental study of meristic characters in fishes. Biological Reviews **27**:169–193.

Thorson, G. 1950. Reproductive and larval ecology of marine bottom invertebrates. Biological Reviews **25**:1–45.

Tsukamoto, K., H. Kuwada, J. Hirokawa, M. Oya, S. Sekiya, H. Fujimoto, and K. Imaizumi. 1989. Size-dependent mortality of red sea bream, *Pagrus major*, juveniles released with flourescent otolith-tags in News Bay. Japanese Journal of Fish Biology **35**(Supplement A):59–69.

Underwood, A. J., and E. J. Denley. 1984. Paradigms, explanations, and generalizations in models for the structure of intertidal communities on rocky shores. Pages 151–180 *in* D. R. Strong and D. Simberloff, editors. Ecological communities: conceptual issues and the evidence. Princeton University Press, Princeton, New Jersey, USA.

Ware, D. M. 1975. Relation between egg size, growth and natural mortality of larval fish. Journal of the Fisheries Research Board of Canada **32**:2503–2512.

West, C. J., and P. A. Larkin. 1987. Evidence for size-selective mortality of juvenile sockeye salmon (*Oncorhynchus nerka*) in Babine Lake, British Columbia. Canadian Journal of Fisheries and Aquatic Sciences **44**:712–721.

Wieser, W., H. Forstner, N. Medgyes, and S. Hinterleitner. 1988. To switch or not to switch: partitioning of energy between growth and activity in larval cyprinids (Cyprinidae: Teleostei). Functional Ecology **2**:499–507.

Wieser, W., and N. Medgyesy. 1990. Aerobic maximum for growth in the larvae and juveniles of a cyprinid fish, *Rutilus rutilus* (L.): implications for energy budgeting in small poikilotherms. Functional Ecology **4**:233–242.

Wilkinson, L. 1990. SYSTAT: the system for statistics. SYSTAT, Evanston, Illinois, USA.

Winemiller, K. O., and K. A. Rose. 1993. Why do most fish produce so many tiny offspring? American Naturalist **142**:585–603.